

Stephen S. Ditchkoff

A decade since “diversification of ruminants”: has our knowledge improved?

Received: 11 October 1999 / Accepted: 6 April 2000

Abstract In his landmark 1989 paper, R.R. Hofmann classified ruminants into three categories based upon digestive anatomy and preferred forages, and proposed that divergence of feeding strategies among ruminants is a result of morphological evolution of the digestive tract. Because of the hypothetical nature of these views and the ingrained beliefs that they challenged, several papers were published that reported tests of Hofmann’s predictions. The consensus among these papers was that Hofmann’s predictions were inadequate. I describe the experimental evidence that has been put forth in opposition to the ruminant diversification hypothesis and contend that we have failed to adequately test Hofmann’s predictions.

Key words Concentrate selectors · Intermediate feeders · Roughage eaters · Rumen bypass · Ruminant diversification

Early attempts to explain variation found in feeding strategies of free-ranging ruminants classified individual species as “browsers” or “grazers” based upon types of forage consumed. Though an important step in understanding the complexities of ruminant nutrition, Hofmann and Stewart (1972) recognized that feeding strategies of ruminants could not simply be classified into two categories, and proposed three categories (i.e., bulk and roughage eaters, selectors of concentrate forages, and intermediate feeders) based upon stomach structure and feeding ecology. Hofmann (1984) later documented variation in all portions of the digestive anatomy among the three categories of his system of ruminant classification. The dynamic interactions among body size, fermentation and passage rates, and energetic requirements, and their influence on dietary strategy formed the basis for these early classifications.

In a landmark paper, Hofmann (1989) expanded upon the concepts proposed by Hofmann and Stewart (1972) and Hofmann (1984) by providing a working hypothesis of the functional and morphological basis for diversity in ruminant feeding strategies. Hofmann (1989) proposed that feeding strategies ranged from nonselective intake of bulk roughage and efficient fermentation in the forestomach, to selectivity for concentrate forages (high in plant cell content) with increased post-ruminal digestion. This hypothesis challenged many beliefs regarding digestion in free-ranging ruminants and proposed that we reexamine the manner in which ruminant herbivores obtain nutrients from the environment.

Because of the magnitude of Hofmann’s hypothesis, several papers (Gordon and Illius 1994, 1996; Robbins et al. 1995) were published describing tests of his predictions. These researchers examined components of Hofmann’s hypothesis and concluded that they did not find support for morpho-physiological adaptations to diet type within classes of ruminants. They attributed differences in digestive function to body mass or food characteristics. As a result, the consensus has been that Hofmann’s hypothesis regarding gut morphology and function in classes of ruminants is inadequate (Robbins et al. 1995; Illius 1997). However, upon critical examination of both Hofmann’s hypotheses and subsequent critiques, I contend that we have not adequately tested Hofmann (1989). Although scientifically sound, the studies of Gordon and Illius (1994, 1996) and Robbins et al. (1995) did not completely examine components of the ruminant diversification hypothesis and therefore should not be considered to support or refute Hofmann (1989).

Hofmann (1989) proposed variations on the traditional theme of foregut fermentation in the ruminant. In addition to suggesting that hindgut fermentation may play an important role in some ruminant animals, he also commented on postruminal digestion of soluble components of the diet after rumen bypass via the reticular groove (Hofmann 1989, p. 448). While post-ruminal fermentation had previously received some attention (Van Soest 1982), selective bypass of the rumenoreticular

S.S. Ditchkoff (✉)
Department of Zoology, Oklahoma State University, Stillwater,
OK 74078, USA
e-mail: steved@okstate.edu
Fax: +1-405-7447824

complex via the esophageal groove, and subsequent digestion of some dietary components in the gastric abomasum and small intestine was a novel idea. However, it was not without basis. Ørskov et al. (1970) found that domestic sheep could be “trained” to allow fluids to bypass the rumen and flow directly into the abomasum, and Hofmann (1973) noted that the reticular groove is well developed in adult ruminants. Hofmann (1984) had previously found that the reticular groove was wider and salivary production greater in concentrate feeders than roughage eaters. If a selective bypass mechanism were present in the ruminant, a nutritional advantage could be realized on some carbohydrate diets by a reduction of rumen fermentation losses in heat and methane following rumen bypass (Ørskov 1986). Potential energetic losses by fermentation of easily digestible forage components can reach 10–20% of available energy (Björnhag 1994; Stevens and Hume 1998). Similar mechanisms have been proposed to explain digestive strategies in some arboreal mammals that rely upon foregut fermentation (Hume and Carlisle 1985; Hume et al. 1988; Cork and Foley 1991; Cork 1996).

Hofmann (1989) also reported that salivary weight as a percentage of body weight, is greater in concentrate selectors than grass and roughage eaters, and Kay (1987) found similar results when examining parotid salivary glands. If rumen bypass of selected forages via the reticular groove does occur in concentrate selectors, then increased salivary production could aid in lubrication and rapid bypass of the rumen and reticulum. The basis of the ruminant diversification hypothesis of Hofmann (1989) is differential digestion of forages both in the rumen and postruminally by concentrate selectors, and his data suggest that there are morphological differences in the digestive anatomy among the categories of ruminants that relate to these digestive strategies.

Gordon and Illius (1994) tested a number of predictions posed by Hofmann (1989) using a dataset of African ruminants. They compared fermentation rates in the fore- and hindgut and estimated volatile fatty acid (VFA) and energy production in grazers and browsers. Although they found no differences in fermentation rates [mol VFA kg^{-1} dry matter (DM) day^{-1}] in the rumen or cecum between classes of ruminants, they noted greater daily energy supplied by VFAs (kJ day^{-1}) in the rumen of grazers than browsers. These data suggest that browsers must obtain greater energy from some other source (e.g., mid- or hindgut) if they are to be as digestively efficient as grazers. Gordon and Illius (1994) found no difference in the energy supplied by VFAs in the cecum, but did not quantify energy absorbed in the small intestine.

Gordon and Illius (1994) also estimated energy supplied by VFAs in the rumen as a function of maintenance. Their model (Gordon and Illius 1994, Fig. 3) indicated that the ability of browsers to meet energetic requirements by rumen fermentation alone was much less than grazers. Assuming equal metabolic requirements and fermentation in the hindgut (Gordon and Illius 1994), then either browsers are less efficient at extracting energy

from their diet than grazers, or browsers obtain energy from a source other than the rumen or cecum (e.g., small intestine). To conclude from these data that “there is little difference in digestive strategy between African ruminants with different morphological adaptations of the gut” is somewhat premature. Although Gordon and Illius (1994) briefly comment on rumen-bypass via the reticular groove, they do not consider this mechanism as a possible explanation for their experimental results.

Robbins et al. (1995) tested components of the ruminant diversification hypothesis by comparing fiber digestion, salivary gland size, resting (non-feeding) salivary flow rates, and ruminal liquid flow rates between browsers and grazers. They found no differences in fiber digestion between grazers and browsers, but similar to Hofmann (1984, 1989) did find that salivary gland size was approximately 4 times greater in browsers than grazers. Robbins et al. (1995) found no difference in resting flow rate of saliva between ruminant classes and concluded that enlarged salivary glands may not serve to increase passage rate of forages through the rumen. However, these data are inadequate for testing the predictions of Hofmann (1989). Hofmann (1989, p. 450) proposed increased salivary production as a mechanism for rumen bypass via the reticular groove while feeding, not when resting as was tested by Robbins et al. (1995). Robbins et al. (1995) also compared ruminal liquid flow rates in grazers and browsers to test for increased passage in browsers. But once again, they did not test the predictions of Hofmann (1989) because he proposed rumen bypass, not increased ruminal flow rates, as a method to transport soluble carbohydrates past the rumen. I believe that the conclusion of Robbins et al. (1995) that “Hofmann’s nutritional and physiological interpretations of anatomical differences amongst ruminants are not supportable” is unfounded because they failed to measure digestive characteristics relating to Hofmann’s hypothesis of rumen bypass via the reticular groove. The conclusion of Robbins et al. (1995) should have neither supported nor refuted Hofmann (1989), because flow rate from the rumen is a measure of passage rate that is likely independent of selective bypass of forages, and resting salivary output should not influence bypass of forages via the reticular groove.

Gordon and Illius (1996) examined the ruminant diversification hypothesis by modeling digestive parameters such as passage, fermentation, and energy-supply rates of both grazers and browsers, and incorporating information relating to body mass and chemical composition of forages. Although their model adequately represents traditional ruminant kinetics and even incorporates cecal fermentation, it does not address the issue of rumen-bypass mechanisms and their influence on energy assimilation. As a result, their data alone can not be used to support or refute Hofmann (1989) because they do not incorporate digestive kinetics of the abomasum and/or small intestine.

I propose that in the 10 years since Hofmann (1989), we have failed to adequately test whether physiological

function varies among ruminants with morphological adaptations to certain diet types. But has our knowledge improved since Hofmann (1989)? Gordon and Illius (1994, 1996) and Robbins et al. (1995) undoubtedly provided data that improved our understanding of ruminant digestion. Yet, an essential component of the ruminant diversification hypothesis, rumen bypass of selected forages via the reticular groove, remains a mystery. As a result, the truth regarding the validity of the ruminant diversification hypothesis eludes us as well. We must determine whether ruminants selectively bypass the rumen via the reticular groove. If rumen bypass is a legitimate physiological mechanism, we must assess its distribution among and value to ruminant feeding types. Finally, we need to estimate if rumen bypass mechanisms can supply enough energy to account for discrepancies that have been found between calculations of energetic intake and requirements. Only after we have addressed these questions can we begin to draw conclusions regarding the ruminant diversification hypothesis.

Acknowledgements I would like to thank E.C. Hellgren for insightful discussion and comments on earlier drafts of the manuscript.

References

- Björnhag G (1994) Adaptations in the large intestine allowing small animals to eat fibrous foods. In: Chivers DT, Langer P (eds) *The digestive system in mammals: food, form and function*. Cambridge University Press, Cambridge, pp 287–309
- Cork SJ (1996) Optimal digestive strategies for arboreal herbivorous mammals in contrasting forest types: why koalas and colobines are different. *Aust J Ecol* 21:10–20
- Cork SJ, Foley WJ (1991) Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defenses in temperate and tropical forests. In: Palo T, Robbins CT (eds) *Plant defenses against mammalian herbivory*. CRC, Boca Raton, pp 133–166
- Gordon IJ, Illius AW (1994) The functional significance of the browser-grazer dichotomy in African ruminants. *Oecologia* 98:167–175
- Gordon IJ, Illius AW (1996) The nutritional ecology of African ruminants: a reinterpretation. *J Anim Ecol* 65:18–28
- Hofmann RR (1973) *The ruminant stomach: stomach structure and feeding habits of East African game ruminants (East African Monographs in Biology, vol 2)*. East African Literature Bureau, Nairobi
- Hofmann RR (1984) Comparative anatomical studies imply adaptive variations of ruminant digestive physiology. *Can J Anim Sci* 64:203–205
- Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78:443–457
- Hofmann RR, Stewart DRM (1972) Grazer or browser: a classification based on the stomach-structure and feeding habits of East African ruminants. *Mammalia* 36:226–240
- Hume ID, Carlisle CH (1985) Radiographic studies on the structure and function of the gastrointestinal tract of two species of potoroine marsupials. *Aust J Zool* 33:641–654
- Hume ID, Carlisle CH, Reynolds K, Pass MA (1988) Effects of fasting and sedation on gastrointestinal tract function on two potoroine marsupials. *Aust J Zool* 36:411–420
- Illius AW (1997) Physiological adaptation by savanna ungulates. *Proc Nutr Soc* 56:1041–1048
- Kay RNB (1987) Weights of salivary glands in ruminant animals. *J Zool Lond* 211:431–436
- Ørskov ER (1986) Future perspectives for the protection of nutrients from fermentation in the rumen. In: Neimann-Sorensen A (ed) *New developments and future perspectives in research on rumen function (ECC Agricultural Series, EUR 10054)*. Office for Official Publications of the European Community, Brussels, pp 217–226
- Ørskov ER, Benzie D, Kay RNB (1970) The effect of feeding procedure on closure of the oesophageal groove in sheep. *Br J Nutr* 24:785–795
- Robbins CT, Spalinger DE, Hoven W van (1995) Adaptation of ruminants to browse and grass diets: are anatomical-based browser-grazer interpretations valid? *Oecologia* 103:208–213
- Stevens CE, Hume ID (1998) Contributions of microbes in vertebrate gastrointestinal tracts to production and conservation of nutrients. *Physiol Rev* 78:393–427
- Van Soest PJ (1982) *Nutritional ecology of the ruminant*. OB Books, Corvallis